Prof: Paget F.R.S. from the Author

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A MAIN CAUSE

OF

DISCORDANT VIEWS

ON THE

STRUCTURE OF THE MUSCULAR FIBRIL.

BY

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[With a Plate.]

I LATELY had the pleasure, on more than one occasion, of examining muscle at Glasgow with Prof. Allen Thomson. The microscope used was one of first-rate excellence by Smith and Beck. We saw the states in Plate V. fig. 2 *ab* and *ikl*—drawings sent me a few days after by the Professor, accompanied by the following description and remarks:—"Portions of three different muscular fibrillæ from the Frog, presenting various aspects. *ab*, a fibril splitting into two at *c*, viz. *cd* and *ce*; the part *ac* is probably double; *ce* and *cd* are single. *db* appears single; but it is possible that it may be double, as *e* seems to have been separated from *c* to *d*. From *a* to *c* the quadrilateral form of the sarcal particles and the clearer intervening substance prevails; in *ce* and *cf* the oval and oblong quadrilateral; from *f* to *d* the rhomboidal; and from *d* to *b* the rhomboidal, with an appearance of spiral or twist in the intervals.—*g* and *h* are portions of another fibrilla, in which the quadrilateral form of the particles, and the distinction between them and the intervals, are particularly well marked; in *g* the upper surface is in focus, and the cross mark in the intervals is not seen; in *h* the focus is adjusted for the deeper or further side, the intervening substance is crossed by a distinct transverse line, and each dark quadrilateral particle presents a central spot, or rather a slightly crucial mark in its centre. Although the portion of fibril here represented appears quite single, I think I can see that at the end a portion of it, not represented in this figure, is split into two smaller fibrils.—*ikl*, two fibrillæ separated at one part and united in another; a dislocation of the particles having taken place, so as to produce an appearance of spiral form even more

distinctly than the drawing represents. *l* seems single; but it may be doubted, from what has been observed in following out other fibrillæ of the same form, whether the part ending at *k* is reduced to its smallest elements. The specimen above described has been preserved for three or four years in the moist state in weak spirit or glycerine, I am not sure which. I think it is one which, along with others, I received from Dr. Dobie *.—A. T."

The Professor adds:—"In the upper figure, *ab*, you will see that I have suggested in the description the possibility of the part from *b* to *d* being double. I am induced to think so, both because *ce* appears to have been separated from *ca* only as far as *d*, and because in several adjustments I have observed the appearance of each particle being made up of two slightly dislocated (a disposition which is slightly indicated in the last particle at *b*). I still admit that the portion of fibril, including these four particles from *b* to *d*, presents very much the appearance of a spiral or twist; but, since it is the only portion among a very great many fibrils in which I have seen the spiral form (that is, a spiral appearance not obviously caused by dislocation, as in *ik*, which, as you know, might mislead), I must in the meantime suspend my judgement as to the cause of this seeming spiral." He further remarks:—"As I stated to you in conversation, I cannot make up my mind as to the nature of this structure;" and adds:—"I shall therefore look with much interest for the more full explanation of your observations." With regard to specimens that I had shown him, sent me by Dr. Thomas Spencer Cobbold †, from the tentacula of the Actinia,—in which he (Dr. C.) had discovered proofs of the accuracy of my views,—Prof. Allen Thomson, after remarking that they present a clear view of the double spiral, adds:—"I admit that if these double spiral prehensile filaments of the Actinia are *contractile*, they may be fairly used by you as an argument in favour of your views." Besides this, the Professor admits "the existence of the spirals very clearly—in the heart."

If all observers were as circumspect in making up their minds as Allen Thomson, science would progress with less of fluctuation. The more full explanation of my observations, for which that distinguished physiologist is good enough to say he shall look with much interest, requires however but very few words.

Divisions such as those we together saw, and which have been most faithfully delineated by him in fig. 2, I had figured in the Edinburgh New Philosophical Journal for October 1843, plate 5.

* Dr. William Murray Dobie, at present one of the house surgeons in the Royal Infirmary of Edinburgh.—M. B.

† Under-Conservator of the Museum of Anatomy and Physiology in the University of Edinburgh.

fig. 2; and in Müller's *Archiv* for 1850*. When subsequently examining, along with the Professor, a preparation sent me by Dr. Dobie, we found several of the states in fig. 4, which fully confirm and extend the observations now referred to as recorded by myself in 1843 and 1850†. For this drawing also (fig. 4) I am indebted to the kindness of Prof. Allen Thomson. It needs no description, affording unquestionable evidence of division and subdivision—changes which observers have overlooked, or at least in their consequences disregarded. These changes, with those seen in fig. 2, and with what I am about to state, furnish the explanation he requires.

There first exists a line of bodies comparable to germinal spots. Each spot divides into halves, and then each half into four parts; so that each spot comes to consist of eight particles, which eight particles lie in two strata—four in each. This is shown by fig. 5 (also from nature, and drawn by Prof. Allen Thomson), the particles in outline representing the upper, and the shaded particles the lower stratum. Dislocation takes place, a change immediately following the division into halves. Of dislocation an example is afforded by fig. 2 *ikl*, which presents a side view. As dislocation proceeds, there arises in the clear space an appearance *which we call a transverse line*. Of this line no satisfactory explanation has yet been given. My belief is that it results from particles belonging to the stratum not in focus. This, I think, is shown by *b* and *c* in the drawings from nature, fig. 4, where it is no longer a mere line that is seen, but there have come into view particles not differing from those of the stratum that is in focus. In harmony with this opinion is the following remark by Prof. Allen Thomson, written by him opposite the drawing from nature, fig. 5, viz. "The transverse line in the clear space is seen when the lower side is in focus; and coincides exactly in the specimen figured with the margin *a* of the square particles when the upper side is in focus."—The line of particles *b*, fig. 4, affords an instance of longitudinal separation, exhibiting one half of such a line as that at *c* in the same figure. There can be no doubt that in these lines we see the smallest elements discernible with our highest magnifying powers.—The line *a* in the same figure (fig. 4) appears to represent a state corresponding to that of the line *b*; but with this important difference, that in

* Taf. XVII. fig. 29. See also Phil. Mag. for August 1852, Plate I. fig. 6.

† Changes such as those in fig. 4 are obviously intimated by the "crucial mark" at *h* in fig. 2. Concerning this crucial mark, the Professor, in a letter I have since received from him, remarks:—"This was well given, if I remember right, in Dr. Dobie's paper." [Published, I hear, in the Annals of Natural History for February 1849; but I have not seen it.—M. B.]

a the particles are flat. Such flattened particles I sketched in Müller's *Archiv* for 1850*, and reproduce the sketch in fig. 3.

In now proceeding to point out the ways, in one or more of which I think it possible that such a line may pass into a spiral form, I would ask a reference to drawings I gave from nature in 1842, after a long-continued examination of the elements of fibre at the earliest period†. For I presume that no one will say that what was seen of the earliest formation of fibre may not be applied in endeavours to throw some light upon its mode of reproduction.

Those drawings show spirals to arise out of piles of particles having a ring-like form. The rings were met with and represented arranged in three ways, viz. 1st, in a single pile, as in fig. 6 A; 2nd, arranged in alternate or overlapping order, as in fig. 6 B; 3rd, connected like links of a chain, as in fig. 6 C. Rings arranged in all these ways were found in piles; and rings arranged in all these ways were seen passing into spirals‡. I further showed the existence of such bodies as that in fig. 6 D §, an altered ring, which if produced must pass into some form of spiral. When each ring of the first arrangement, A, assumes the form D, union of the extremities of a pile of bodies such as D forms a single spiral, and this by longitudinal division passes into two, as in fig. 6 E ||. When, according to the second arrangement, the rings overlap each other, as in fig. 6 B, or, according to the third arrangement, are connected, as at C, the union of the extremities of a pile of such bodies as that at D is attended with interlacement, forming at once the twin spiral E.

[Of this twin spiral a drawing from nature (Heart of Frog) is seen in fig. 7. It represents neither full contraction nor complete relaxation, but four intermediate states; and these were seen at different parts of the same fibril. As the two spirals run in the same direction, *i. e.* as they are parallel, I have been accustomed latterly to term this fibril, and indeed all organic fibre, a *twin* spiral¶.—In all three of the arrangements I showed the rings to have become segmented, as in fig. $7\frac{1}{2}$ *b*, an appearance of course familiar to all accustomed to examine the elements of tissues. The segments intimate the formation of the particles

* Taf. XVII. fig. 29.

† Phil. Trans. 1842, plate 7, figs. 45 to 48.

‡ Phil. Trans. 1842, plates 6 and 7, figs. 31–33, 47, 48.

§ Phil. Trans. 1842, plates 5, 6 and 11, many figures.

|| Fig. 6 E represents an apparatus for constructing a model of the twin spiral muscular fibril, to be explained further on.

¶ I had previously called it a *double* spiral; but this seems not so fully to imply that the direction of the two spirals is the same. [Originally I believed their directions to be different, but corrected the error in Müller's *Archiv* for 1850, and in the Phil. Mag. for 1852.]

of which spirals are composed*.—The pellucid centres of the rings are left as elements of future offspring, to assume the form of spirals when their progenitors the old spirals as contractors are worn out.]

What has just been referred to as seen of the mode of origin of the muscular fibril, I would now apply in considering its mode of reproduction.

Thus the flat particles in fig. 4 *a* I apprehend to be in a state resembling or approaching that of rings. They are, in fact, bodies of the same form as mammiferous blood-discs, fig. $7\frac{1}{2}$ *a*. Each has its pellucid centre or nucleolus, which, when the outer part assumes the spiral form, is left behind—a line of such nucleoli being the foundation of future offspring.

Now I have no doubt that *a*, fig. 4, passes into a twin spiral in one of the ways just described. If in the first way, it probably undergoes longitudinal separation into two single piles such as that in fig. 3; and then each pile forms a single spiral, which by longitudinal division becomes a double one. But if *a*, fig. 4, assumes the spiral form in either of the two other ways, it undergoes no longitudinal separation, and it forms but one twin spiral.

It is obvious that the bodies *df*, fig. 2, pass into the bodies *bd* in the same figure. The question is: what is the condition of *bd*? Prof. Allen Thomson believes it to be double. I am of the same opinion. Even he admits it to present "very much the appearance of a spiral." And here also agreeing with him, I would direct attention to a change in the direction of the transverse line in the clear spaces, which direction in *bd* crosses that of the transverse line in *df*. It may therefore be that *df*, fig. 2, consists of two strata of particles, which particles come to alternate with, or overlap one another, as at B in fig. 6; and that further changes, such as those just described, produce an approach towards the completion of a twin spiral in fig 2 *bd*.

Whether, however, an approach towards the completion of a twin spiral is or is not exhibited in the fibril seen by Prof. Allen Thomson and myself, and delineated by him in fig. 2 *bd*, I certainly saw a twin spiral at the upper end of the fibril in fig. 1. This figure I published in the Edinburgh New Philosophical Journal for October 1843, plate 5. fig. 2†. And as it exhibits three states, viz. that of quadrilateral particles (*c*), division and dislocation of these (*b*), and then *as a continuation of the latter*

* Phil. Trans. 1842, plate 10, fig. 125. I also showed, by the action of acetic acid, that spiral filaments are made up of particles. (Phil. Trans. 1842, plate 8, fig. 68.)

† It represents a young fibril of muscle from the ventricle of a frog's heart; drawn as magnified 600 diameters.

the twin spiral (*a*) in the same fibril, I have thought the figure deserving of reproduction here (fig. 1). Along with this figure I published the following remarks, viz. "Were filaments formed by each half-nucleus (fig. 1 *b*) of two adjacent rows to assume the spiral form and interlace, and the filaments of the same row to then unite, we should have the double spiral. [The oblique position of the two rows of half-nuclei in fig. 1 *b* is not undeserving of notice here.]*"

It is satisfactory to find, that while the renewed inquiries made known in this communication enable me to explain some details, they do not show that views thus long since published require an essential change.

A friend, long accustomed to use the microscope, and gifted with a keen microscopic eye, whom I had convinced of the existence of spirals in muscle, once suggested that the spiral structure might "be the earlier rather than the fully-developed condition of the fibril, the quadrilateral particles representing its fully-formed state." Referring him to the drawing reproduced in fig. 1, I was compelled, with almost rude brevity, to say that I should find it about as easy to admit that thread exists before the flax that forms it, or a chain before the links of which it is composed.

Consisting as it does of two spiral filaments, the muscular fibril, in its movements between contraction and relaxation, of course presents a variety of forms. And as the microscopic inquirer into the structure of muscle is sure to have one or more of such forms before him (unless all the muscle in the field of view is in full contraction or complete relaxation), I have constructed models by which the eye may be prepared for these forms.

In fig. 6E is shown a very simple method of constructing such a model. At *a* are two lead wires of equal length, which, held parallel and together, were obliquely wound upon a large knitting needle, *b*. The needle having been withdrawn, there remained a model of the mature and acting muscular fibril (and indeed of the original form of all organic fibre). So easily did the two wire spirals then change their positions, that on merely rolling the model on a white surface, I saw it present the three varieties of form *a*, *b*, *c*, drawn from nature in fig. 7; which include two states of the single and one of the double cylinder.

While, however, from their weight, wires of lead have the advantage just mentioned of presenting changes in relative position

* Edinb. New Phil. Journal, Oct. 1843, p. 214.

on the model being simply rolled, they are not elastic. I therefore used wire of gutta percha, fig. 6 F. At *a* in this figure is a bit of small wire of gutta percha. This I bent upon itself at *c*; and then, having firmly tied with thread the loop *c* to a knitting needle *b*, I wound the double wire upon the needle in a direction almost *as nearly transverse as possible.* Then, keeping firm pressure applied by the finger and thumb at the lower ends of the wires, I plunged the wires for a few seconds into water of about 130° Fahrenheit (44° Reaumur*). Thus softened and deprived of their elasticity, the wires were slipped off the needle. In a few seconds they had hardened and recovered their elasticity. After having been minutely examined for the detection and breaking up (with a needle) of adhesions that might have occurred in the softening, the wires were gently extended, and found to spring back into the previous comparatively contracted state; thus beautifully illustrating the movements of the muscular fibril. The union seen in this model of the two spirals at the end of the fibril, is to be inferred from analogy with what I have elsewhere shown in cilia.

I cannot refrain from once more recommending *the heart of some reptile* as especially adapted for the examination of the fully-formed muscular fibril. The heart of the Turtle has often afforded me unquestionable specimens of the twin spiral†; but far more easily obtainable is that of the common Frog.

In order thoroughly to understand the structure of this tissue, however, it is essential to see it in its most incipient state, and patiently to follow it through every stage. At that early period its elements are very large, of course an immense advantage to the observer. I had this advantage; and using, as I for the most part did, the larva of the large Jersey Toad (which a friend informs me is a variety of the common Toad), I had a further advantage, the first elements of muscle in that larva being of enormous size. Out of these I saw spirals to arise of corresponding size; so large as to enable me not only to discern the particles of which they were composed‡, but also to observe that by division and subdivision spirals pass into membrane, forming for instance the sarcolemma, the cells of cartilage and the cells of coagulating blood. [An observation confirmed ten years after by Agardh, who in his paper *De cellula vegetabili fibrillis tenuissimis contexta*, Lundæ, 1852, shows not only that vegetable membrane is formed by fibre, but that the fibre forming vegetable membrane has the very structure that I maintain to be that of

* If the water be too hot, the wires over-softened adhere together.
† See, for instance, in the Phil. Trans. for 1842, plate 7, fig. 56.
‡ Phil. Trans. 1842, plate 8, fig. 68.

all organic fibre, being composed of spirals which in number he delineates as two, and moreover represents as dividing—each of them into a fasciculus of spirals*.] And of course I refer to spirals the gentle undulations which constitute the first movements of the Tadpole's tail; in other words, I conclude that it is the spirals that are endowed with contractile power; for to what else is to be attributed this power where all that can be recognized as muscle is made up of spirals?

The eye, when thus accustomed to spirals of large size, discerns them though exceedingly minute, as in older muscle. Here observers, not thus prepared, mistook the winds of spirals for varicosities or beads; for instance, Bowman, who in single fibrillæ figures as such what were evidently spirals†. Some of his delineations of fasciculi, also, afford beautiful illustrations of spirals distorted in manipulation, of which the appearance he aptly compares to "engine-turning" is an exquisite example. I can attest the accuracy of those delineations of fasciculi. They are faithful representations of nature; but, at the same time, they are proofs of the existence of a structure, which for the reason just mentioned the delineator did not understand. As for the "discs" of Bowman, they are transverse slices of fasciculi *in full contraction*, cut off where least capable of withstanding violence in manipulation. At such parts each spiral of a pair is then in contact with its fellow; there they cross and antagonize each other; *in full contraction this crossing is at the acutest angles, and consequently there they cut each other through.* And if maceration has been used, a practice too common with some observers, no wonder if the "discs" present little more than particles; for *it is of particles that the spirals are composed.*

How true the words of Huschke, that "in order to understand an organ or the structure of a tissue, we must inquire: *How did it originate?*" When muscle, a tissue more complicated than any other, has been thus dealt with by observers generally, they will understand and acknowledge its spiral structure; *but not till then.*

Since Bowman wrote, observers, in their endeavours to reach the *ultimate* structure of the muscular fibril, have actually gone too far. They passed over what really admits of examination—the mature fibril, and arrived at what almost defies the microscope—its embryo; mistaking and delineating for the fibril a row of quadrilateral particles, the mere elements thereof; mis-

* Agardh, *loc. cit.* Tab. I. fig. 8.

† Phil. Trans. 1840, plate 16, figs. 10, 12, 15, drawings copied by myself into Müller's *Archiv*, 1850, Taf. 17, and into the Phil. Mag. 1852, Plate I., for the purpose of showing them to represent spirals.

taking for the chain, as it were, a row of half-formed links destined to compose the ehain. It is not surprising, that, as the embryo fibril passes through many stages in the course of its development, it should have presented different appearances to different observers, producing a corresponding varicty of deserip-tions and drawings. And I certainly cannot wonder that in a row of quadrilateral particles no one could diseern my twin spirals! Without therefore questioning the aceuraey of these observers in describing and delineating what they saw, I maintain, in the first plaee, that it was impossible for them to agree with one another; and seeondly, as our attention was directed to two very different things, that it was still less possible for any of them to agree with me. Hencc a main eause of dis-eordant views on the strueture of the museular fibril.

FURTHER REMARKS

ON

THE MUSCULARITY OF CILIA.

BY

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[With a Plate.]

THE Philosophical Magazine for August and September 1852 contains the substance of a paper of mine which had been translated into German from the English MS. by Prof. Purkinje, Foreign Member R.S., and communicated by him to Müller's *Archiv* for 1850; confirming by renewed inquiries, made in his house, the observations I had recorded in the Philosophical Transactions eight years before (1842) on the spiral structure of muscle, and announcing the muscular character of cilia. It was in bivalve Mollusca and in Infusoria that I saw the latter.

Arisen like independent beings each in its own cell or ovum, and endowed with contractile power, cilia of the Mussel's gill were shown to grow and pass through stages of development both in action and in form; and at length, when matured, and not till then, to combine in large numbers for the production of a current. A pellucid membranous canal, apparently destined to absorb oxygen from the water, was seen to exhibit on each side a phalanx of cilia (Plate V. fig. 10 *n*, *o*); while the extremities of these, arching over, united to form an avenue through which by their vehement undulatory vibrations to drive a stream, and thus arterialize the blood. It was further shown that young cilia (*m*, in the same figure) are continually arising to take the place of those that drive the stream; the latter, when worn out, being one after another cast off and swept away by that same stream, to be succeeded, as just said, by fresh generations, which produce and in their turn undergo like changes. My observation of continued renewal of muscular fibrils in the ever-acting heart, was thus confirmed by what I subsequently saw of continued renewal among incessantly vibrating cilia.

I have now to add, that, arising coil-like from the nucleus of a cell, the young cilium pushes forth the cell-wall, as in the outline fig. 8, to some little length before the extremity is free, often giving to its cell the flask- or retort-like appearance I formerly described as produced in blood-cells of one of the Amphibia, from a like pushing forth of the cell-wall by the fibre given off by the nucleus in those cells. And when the extremity of the cilium is free, fig. 9, there is still to be recognized in the bent form of young cilia a trace of that in which the nucleus gave them off.

Every cilium is a twin spiral, like the muscular fibril. Fig. 9, a drawing from nature, represents a young cilium from the gill of the common Oyster, in the form in which it proceeds from its cell. At the extremity its two spirals pass into one another, and are bent over hook-like towards one side. At the base they separate, to bestride as it were a bulb consisting of minute pellucid globules of high refractive power. These globules I have elsewhere termed the contents of the cell, and such they are. More particularly considered, however, they represent the remains of the *nucleus* of the cell resolved into globules. The two after-threads derive their nourishment from, or rather they are formed by the globules in the bulb. The bulb thus gradually becoming exhausted diminishes in size, and at length entirely disappears. Hence it was that I found the bulb at the base of some cilia much smaller than at that of others. Hence, too, an explanation of the cause why some observers have denied the existence of a bulb; their attention having probably been directed to cilia from which the bulb had disappeared.

The two after-threads may perhaps be considered as the roots of the cilium, in which it has its early growth. The extremity of each of them takes up new substance from what had been the nucleus of the cell, while the cilium, by its rotatory movements, which consist in twisting and untwisting (contraction and relaxation), spins up the after-threads—its early mode of elongation. For this the after-threads are prepared by their spiral form, which also seems to be a provision for rendering the elongation of the cilium rapid. It will be seen from the figure that each after-thread is a single spiral, being twisted on itself; and that the direction of the spiral winds is in both of them the same; the same, moreover, as that of the twin spirals of the cilium of which the after-threads are continuations. Very few movements, therefore, of the kind just mentioned sufficed to apply to one another these after-threads, and thus to make them part of the cilium itself.

I have presented a model in lead wire of the muscular fibril,

and of a young cilium such as that in fig. 9, to the Royal Society, to the Museum of the Royal College of Surgeons in London, to the Royal Society of Edinburgh, to various colleges and museums in Edinburgh, and to the Museum of Physiology in the University of Prague.

Along with the model of a young cilium presented to the Prague Museum, I left the following remark, translated into German by my honoured friend Prof. Purkinje:—"From analogy it appears extremely probable that the heart arises in like manner out of the nucleus of a cell, being originally such a double spiral [as that in fig. 9]. If so, the spiral form of the heart may be explained by the continued division of what was originally a double spiral fibre."

To the subject of self-division, as part of the process of reproduction, more importance will by and by be attached than heretofore. For as the properties of the simplest form of separate independent locomotive Infusoria descend to it from progenitors by fission,—by the same fissiparous mode it appears to me do properties descend from cell to cell, or rather from nucleolus to nucleolus, though these are not separate but combined, and merely parts of a more complicated organism. Having made known my observations on this subject in Müller's *Archiv* and in former numbers of this Journal*, I have here merely to repeat, for the purpose of applying it to the suggestion referred to concerning the heart, that the filaments of all organic fibre are made up of particles (nucleoli), and that these particles, and therefore the filaments of fibre, are reproduced in no other way than by self-division†.

* Müller's *Archiv*, Heft vi. 1850. Phil. Mag. August and September 1852.

† See a paper of mine in the Edinburgh New Philosophical Journal for October 1853, "On Animal and Vegetable Fibre."